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Soft-bodied fossils are not simply rotten carcasses—towards a holistic understanding of exceptional fossil preservation

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Subtitle

Exceptional fossil preservation is complex and involves the interplay of numerous biological and geological processes

Abstract

Exceptionally preserved fossils are the product of a complex interplay of biological and geological processes including burial, autolysis and microbial decay, authigenic mineralization, diagenesis, metamorphism and finally weathering and exhumation. Determining which tissues are preserved and how biases affect their preservation pathways is important for interpreting fossils in phylogenetic, ecological and evolutionary frameworks. Although laboratory decay experiments offer a means of investigating important aspects of fossilisation, applying the results directly to the interpretation of exceptionally preserved fossils may overlook the impact of other key processes that remove or preserve

morphological information. Investigations of fossils preserving non-biomineralized tissues suggest that certain structures that are decay resistant (e.g. the notochord) are nonetheless rarely preserved (even where carbonaceous components survive), and conversely, decay prone structures (e.g. nervous systems) can fossilize, albeit rarely. Decay resistance is only a partial proxy for fossilization potential and a suite of biological and geological processes account for the features preserved in exceptional fossils.

Introduction

Most of the species that ever existed are extinct, and the vast majority will never be known as fossils. This is because fossilisation, even of organisms with mineralized skeletons, is a rare event and few taxa enter the sedimentary record; likewise few sedimentary sequences survive subduction, or uplift and erosion, to be sampled for fossils [1]. The bulk of the fossil record consists of those parts of organisms that are most resistant to degradation – shells, bones and teeth. In some cases shelly fossil remains are so abundant that thick accumulations form entire rock units – chalk, for example, is composed of the calcium carbonate plates of unicellular eukaryotes called coccolithophores. Soft parts, in contrast, are usually lost through scavenging and decay.

In rare cases the soft (i.e. non-biomineralised) parts of animals survive and are fossilised alongside the hard skeleton, and even wholly soft-bodied organisms (those without biomineralised tissues) can be preserved. The journey of these fossils from death to discovery involves a complex interplay of geological and biological processes (Fig. 1) and although they are rare, they offer unique insights into the anatomy and biology of extinct life (Fig. 2). Such 'exceptional' deposits are commonly referred to as 'Konservat-Lagerstätten' [2] – literally 'mother lodes' – a German term that is now common currency among palaeontologists (Lagerstätte is borrowed from the mining industry where it means an ore body or 'mother lode'). Konservat-Lagerstätten occur throughout the geological record in a diversity of palaeoenvironmental settings and

sedimentary rock types [3]. Soft parts can be preserved in a variety of ways: as carbonaceous compressions (Fig. 3B), via early (authigenic) mineralization in iron sulphide (pyrite) (Fig. 3C) and apatite (calcium phosphate) (Fig. 3D), and by early cementation or entombment, such as in concretions (Fig. 3E) or within amber. Within a single specimen, a combination of these preservational pathways can account for the preservation of the whole organism, with different tissues following particular preservational pathways. For example, Figure 3F shows scanning electron microscope energy dispersive x-ray (SEM-EDX) maps of a specimen of *Marrella splendens* from the Cambrian Burgess Shale of British Columbia, which preserves certain anatomical features as carbon films, pyrite or calcium phosphate.

The Burgess Shale is one of a number of well known examples of exceptional preservation which reveal diverse assemblages of early animals [4,5]. Other examples of exceptionally preserved biotas include the plants and animals found in the Carboniferous Mazon Creek concretions of Illinois [6], the fishes that preserve phosphatised subcellular details of muscle tissue in the Cretaceous Santana Formation concretions from Brazil [7], and the feathered dinosaurs that reveal evidence of plumage colour and flight capability from the Cretaceous Jehol sequences of north-eastern China [8].

Despite the diversity of settings that yield exceptionally preserved fossils, many Konservat-Lagerstätten share biological and geological processes such as rapid burial, limited or no bioturbation, decay suppression through anoxia or euxinia, and sealing of sedimentary laminae with microbial mats and early diagenetic cements (Fig. 1). These factors contribute to the survival of organic macromolecules [9,10] and create the necessary microenvironments for the replication of soft tissues through authigenesis, the early precipitation of minerals [11]. Understanding preservation (the field of taphonomy) is critical to interpreting the morphology of fossils and, in turn, their place in the tree of life and consequent significance for organismal evolution. A first step is determining which characters were originally present and which have been lost or modified by taphonomic processes [12]. A second step involves recognising possible homologies between features of the fossil organism and those of living taxa

[12,13]. The identification of homologies is essential for determining the affinity of fossils, but it is particularly challenging in cases where there is no obvious close living relative.

Rather than representing perfect snapshots of extinct organisms, soft-bodied fossils have passed through numerous filters on their journey from death to discovery that remove, modify, or preserve anatomical characters (Fig. 1). Such processes include autolysis (self digestion through enzymes) and microbial decay, precipitation of authigenic minerals, diagenesis (plus metamorphism in some cases), and finally weathering (Fig. 1). The pathways travelled by exceptional fossils prior to discovery are complex, and understanding preservation is an active field of research based on investigations of fossil specimens and actualistic experiments [14]. Following discovery, further biological information can be lost or modified during excavation and preparation of a fossil; the method used to remove surrounding matrix may create artefacts and should be taken into account when analysing important features [15,16].

A key hurdle to interpreting fossils correctly is determining which characters are missing because they were originally absent *in vivo* and which characters have failed to survive all of the processes involved in fossilisation. Decay experiments have played a central role in interpretations of soft-bodied fossils for many years, illuminating the relative preservation potential and likely identity of different soft parts in fossils, determining the conditions required for the replication of tissues in authigenic minerals, and documenting how the molecular components of an organism are impacted by decay [17]. More recently, however, there has emerged a tendency to apply the results of decay experiments more literally to the interpretation of soft-bodied fossils, using the relative susceptibility of morphological characters to decay as a measure of whether or not they could be preserved at all [18-20]. While an experimental approach is important to determining how exceptional fossils are formed [21] microbial decay is just one of many processes that can distort the original morphology of an organism. A variety of interlinked processes play a role in the preservation of different anatomical features.

Cambrian fossils from Burgess Shale-type localities have featured most prominently in discussions of how decay determines the information preserved in exceptional fossils, as many Cambrian animals are difficult to place with confidence in a phylogeny with modern groups. The phylogenetic position of early chordate-like fossils, for example, has attracted particular attention following the proposal of 'stemward slippage' [22]. As chordates decay, characters have been described as being lost in the opposite order to their stepwise acquisition during the evolutionary transition from the chordate stem lineage to the vertebrate crown: the farther decay progresses the more 'primitive' the resultant fossil appears. Reports of organically preserved neural and circulatory [23] tissues in Cambrian panarthropods have proved particularly controversial as an interpretation based on stages of decay [18-20] implies that such decay prone features should not persist and fossilise.

Here we review the diversity of processes that occur during fossilisation and identify circumstances where the sequence of character loss and modification in fossils may deviate from the null model provided by the decay of related living animals in seawater [24]. Clearly it is important to avoid overinterpretation of features in a soft-bodied fossil based on a simplistic comparison with the anatomy of its nearest living relative, but equally, the evidence of the fossils themselves should not be dismissed without good cause. In some cases features that are decay-resistant do not survive diagenesis, while others that are decay prone preserve readily. Such considerations challenge the assumption that that the relative decay resistance of morphological characters alone can be used to interpret the morphology of soft-bodied fossils [18].

The advantages of being buried alive

In order to survive the test of time, organismal remains need to be shielded from the natural processes that degrade them. Burial is common to nearly all fossils, although remains may survive on a geologically short timescale in caves or bogs, for example. The impact of burial depends on factors such as rate and type of sedimentation, availability of oxygen, and subsequent cementation and

compaction. Deep burial in a single event, such as a storm, enhances the chances of exceptional preservation particularly where low levels of oxygen inhibit scavenging and destruction by macro- and micro-organisms. Carcasses typically survive on the seabed only where scavengers are absent, as in the famous Ediacaran biotas [25], which predate the major radiation of scavenging and macrophagous animals in the Cambrian (Box 1).

Rapid burial creates a microenvironment around a carcass where bacterial activity rapidly consumes available oxygen. The anaerobic processes that follow may generate conditions that favour the precipitation of authigenic minerals [26,27]. Anaerobic conditions also protect organic substances from oxidation, and reactive substances, such as hydrogen sulphide, may be generated which can stabilize organic materials further (see below). Generally, the more fine grained the sediment the better the preservation of soft tissues because clay and silt limit the rate of diffusion and promote the establishment of chemical gradients around a carcass [28,29]. Such gradients also form where a microbial mat and early diagenetic cement seal in the buried organism (Box 1): this may allow preservation in coarser sediment – even in sandstones in the case of Ediacaran assemblages [30,31]. Sediment mineralogy, particularly of clays, may also play a role in tissue stabilisation [14,28,29,32].

Early cementation of the surrounding sediment promotes exceptional preservation by eliminating pore space and may create a cast of soft tissue anatomy. Early precipitation of carbonate at the sediment surface [33] or the presence of microbial mats [34] may have promoted preservation in Burgess Shale-type deposits, for example, and microbial mats are a common feature of deposits preserving muscle tissue [35]. In other cases a concretion may form around a carcass, preventing collapse and promoting mineralisation. The three-dimensional fossils of the Silurian Herefordshire Konservat-Lagerstätte, for example, preserve remarkable details in carbonate nodules within a volcanic ash (bentonite) which was deposited on the seafloor [36]. Silica precipitates as chert in other settings, providing a medium for preserving carbonaceous fossils: notable examples include early prokaryotes and eukaryotes of Precambrian age

[37], and one of the oldest terrestrial freshwater ecosystems associated with a hot siliceous spring in the Devonian Rhynie Chert of Scotland [38].

Flattening during and following burial is not equivalent to the squashing that characterizes road-kill, although fossils are often are said to look like one. Fossils collapse as a result of decay but their outline is maintained by the confining sediment – lateral expansion due to pressure from above is not the norm. Even highly compacted vertebrate fossils which preserve soft tissue outlines show little evidence of lateral expansion [39,40]. Flattening a fossil on a bedding plane is more like projecting a three-dimensional object onto two dimensions, as in a photograph [41]. Specimens of the same animal buried in different orientations, such as the fossils from the Cambrian Burgess Shale (which were transported in turbulent flows), can be used to inform a three-dimensional reconstruction [41].

Decay experiments in sea water show that information loss is the norm

Although fossilised muscle tissue was first recognised in a Jurassic coleoid cephalopod over 170 years ago [21], systematic investigation of the role of decay in the preservation of exceptional fossils has only been a major topic of research in the last few decades (see supplementary table 1). Earlier studies involved observations on vertebrates in natural or laboratory conditions, with little control on variables, and often took advantage of natural deaths in marine settings [42,43]. One focus was the effect of a decaying organism on the surrounding micro-environment, as in concretion formation [44,45]. Observations of a decaying priapulid were used to interpret Burgess Shale specimens of the Cambrian priapulid *Ottoia* [46]. It was not until the late 1980s, however, that experiments started to explore the impact of various controls on decay [47-49]. These early laboratory experiments showed that decay can proceed rapidly even under anoxic conditions, leading to the realisation that authigenic mineralisation is necessary to retain the morphology of certain decay-

prone soft tissues [49] (for a summary of decay experiments in the literature, see Supplemental information).

A series of decay experiments carried out in the 1990s attempted to monitor and control the complex variables involved as well as exploring the impact of different experimental conditions on morphological decay [50-57]. Annelids and arthropods decaying under different conditions of oxygen and temperature, for example, showed consistent patterns of morphological decay, reflecting the nature of their tissues [53-56]. Interpretations of soft-bodied fossils were informed by which features were more likely to survive decay versus those that degraded rapidly [50,58]. Observations of decay of the lancelet *Branchiostoma lanceolatum*, for example, were used to argue that the axial lines preserved along the trunk of conodonts represent the notochord, and that the apparent offset position of the conodont elements below the head reflects the decay of the supporting tissue [54]. The same decay experiments allowed the chevron-shaped structures in *Conopiscius*, a Carboniferous chordate, to be interpreted as myomeres rather than external scales, and also indicated that a decay-resistant cuticle was not necessarily present in *Pikaia* from the Burgess Shale [54,59].

Decay in seawater has now been monitored in a range of taxa in laboratory experiments (see supplementary table 1): anthozoans [60], annelids [52], chaetognaths [61], priapulids [20], onychophorans [19], pterobranchs [62], enteropneusts [63], non-vertebrate chordates [22] and cyclostomes [64]. Thus the sequence of character loss has been determined for taxa representing most clades of eumetazoans. Despite the diversity of body plans analysed in these experiments, collectively they show that different tissues decay at different rates, with some common patterns of decay proneness across different organisms, and different character systems are lost at different stages in the decay process. Gut, muscle and nervous tissue, for example, are among the first to decay in a broad range of taxa in decay experiments [19,20,52]

The majority of recent experiments were carried out in the absence of sediment in order to facilitate observations of the sequence of decay stages and to reduce the number of variables involved in the experiments. The sedimentary

environment in which a carcass is buried is an important control on decay. The chemical gradients that form may stabilize organic substances or induce mineral precipitation, and the sediment supports decaying tissues and prevents the organism from disarticulating. Decay experiments that incorporate sediment reveal a role for sediment chemistry in soft-tissue preservation, where different clays, for example, may promote the preservation of some tissues but not others [32].

During decay experiments, certain structures persist for weeks or even months. Notable examples are the jaws and chaetae of nereid polychaetes [52], the notochord and myomeres of chordates [22], and the chitinous parts of non-arthropod ecdysozoans such as the claws of onychophorans [19] and scalids of priapulids [20]. Despite the apparent decay resistance of these structures, however, they are not always preserved in fossils. The jaws of nereid polychaetes, for example, do not survive diagenesis despite being heavily sclerotised: they only survive in recent sediments [65], whereas the jaws of other polychaetes occur abundantly as fossils [66], Somewhat counter intuitively, polychaetes that mineralise their jaws are absent or rare as fossils as they are more weakly sclerotized, allowing their mineral components to disaggregate [65]. Similarly, the notochord is absent in fossils of some members of the vertebrate crown group [67] despite its decay resistance.

The molecular composition of tissues and their decay environment influence preservation potential

Structural tissues, such as the exoskeleton of arthropods and the non-biomineralised jaws of polychaetes, are often fossilised even though, unlike shells, they often do not contain biominerals. These carbonaceous fossils are composed of recalcitrant biomolecules, i.e. their molecular composition protects them from decaying or breaking down rapidly and allows them to survive elevated temperatures and pressures. The collagen in notochords and the keratin in claws, feathers and hair are decay resistant, but do not survive geological maturation [68]. In some cases biomolecules may remain as

biomarkers in the rock when all morphology is lost [10]. Bond strengths, functional groups, and steric effects influence the susceptibility of different biomolecules to degradation [9]. Nucleic acids are the least stable, followed by proteins, carbohydrates, lipids, pigments, and structural macromolecules [9,10]. Under certain conditions it is possible to recover more resistant biomolecules associated with fossils in a nearly intact state. Recently, for example, sterols have been reported in a 380 million-year-old Devonian crustacean preserved in a concretion [69] and nearly intact melanin in a 200 million-year-old coleoid cephalopod [70]. But, just as decay resistance is an incomplete guide to the preservation potential of soft tissues, in most cases carbonaceous material must undergo diagenetic modification to survive [71].

Labile molecules may be stabilised by reactions that occur during fossilisation, including processes equivalent to tanning, caramelisation and sulphurisation (vulcanisation). Tannins are polyphenolic compounds with multiple hydroxyl and carboxyl groups that react with proteins and their constituent amino acids in a process similar to tanning, as in the leather industry. Tanning was invoked as an explanation of the survival of polychaete and shrimp carcasses in experiments with clays [32]. Caramelisation, well known in cooking, involves anhydrous reactions between sugars and amino acids in Maillard-type condensations to form melanoidin compounds. Melanoidins have been reported in fossil molluscs and brachiopods [72,73] and are important in the formation of humic acids and kerogens [74]. The reaction of proteins with saccharides to form melanoidin complexes may also explain the preservation of skin in human bog bodies [75].

Sulphurised molecules are a significant component of kerogens and asphaltenes [76,77]. Sulphurisation involves the formation of sulphide and disulphide bridges in a manner reminiscent of the vulcanisation of rubber. The preservation of bone marrow and muscles in amphibians from Miocene sulphur-rich lake deposits in Spain has been attributed to this process [78,79]. Analyses of older fossils, complemented by maturation experiments, have shown that over time the composition of animal and plant cuticles, for example, is transformed by cross-linking reactions into more stable longer chain hydrocarbons (*in situ*

polymerization), which incorporates lipids [80], a process enhanced in the presence of sulphide. This diagenetic change is time dependent, but accelerated by the elevated temperatures experienced by rocks at depth, and although it modifies the original chemical composition and internal structure of tissues, their external morphology remains largely intact [10].

We have a general understanding of the chemical processes involved in the fossilization of soft tissues, but the details of how preservation is affected by the composition of specific tissues and the nature of the microenvironments that develop within a buried carcass are largely unknown. Such an understanding is hampered by the need to deconstruct the extensive chemical alteration that fossilised soft tissues have undergone in order to determine the processes involved. It has been clear for some time, however, that the resistance of molecular components to microbial degradation (selective preservation) is an inadequate explanation of the survival of organic matter in sedimentary rocks and, consequently, of the fossilisation of soft tissues [71,80].

Authigenic mineralization saves tissues apparently doomed to decay

Authigenic mineralization provides a mechanism for fossilising decay-prone tissues before they are lost. The key pathways are (1) phosphatisation, which preserve soft tissues at high fidelity, (2) pyritisation, which retains less fine detail but played a critical role in a number of famous fossil Konservat-Lagerstätten, and (3) templating by clay minerals.

Features known to be preserved through phosphatisation include microbes [81], cells and embryos with possible nuclei [82], guts [83], epidermis [79] and muscles [50,81,84,85]. Experiments have revealed the importance of microbial activity in releasing phosphate and generating the necessary geochemical gradients to induce phosphatisation in a decaying carcass. Sufficient calcium and phosphate ions must be available and pH must drop in order for calcium phosphate to precipitate instead of calcium carbonate (i.e., the 'calcium carbonate/phosphate switch') [26]. Such a decrease is a normal result of

bacterial decay [28,29,52], but phosphatisation tends to favour the preservation of particular tissues and taxa [84,86].

Decay experiments have shown that phosphatisation occurs on a laboratory time scale and is not necessarily restricted to a few unusual settings [50]. Microbial activity promotes decay, destroying morphological information in soft tissues, but it is also essential to establishing the conditions that lead to the replication of soft tissues in authigenic minerals [51,87-90]. The nature of microbial controls is subtle and poorly understood. For example, different species of the same genus of bacteria have been shown to degrade soft tissue on the one hand and replicate cellular organisation and morphology on the other, providing a potential pathway for mineral replication of soft tissue features [14,91,92].

Authigenic mineralisation varies with conditions and between taxa. The fidelity of preservation differs in different muscle tissue types, for example [84], mineralization of soft tissue is rare or absent in some taxa even where they occur in association with others that are heavily phosphatised [84], and some taxonomic groups are not represented in the fossil record due to taxon-specific effects during decay [93]. The longitudinal and parapodial muscles of the Cretaceous amphinomid polychaete *Rollinschaeta myoplena* are preserved with greater fidelity than other muscle groups although muscle tissue is rarely preserved in associated polychaetes, and only with low fidelity [84]. These differences may reflect specific properties of amphinomid muscle, such as greater density or availability of phosphate compared to other polychaetes. Circular muscle may be preserved with less fidelity than other muscle types, based on the evidence in fossil annelids [84], or the presence of these muscles may be uncertain due to poor preservation, as in the gilled lobopod *Pambdelurion* from Sirius Passet [94]. The absence of phosphatised soft tissue in fossil decabrachian cephalopods has been shown experimentally to be due to the presence of ammonia for buoyancy regulation, which prevents the drop in pH necessary to allow phosphatisation [93]. An understanding of the controls on phosphatisation is therefore important for constraining interpretations of authigenically mineralised soft tissues.

Authigenic mineralisation can upend the sequence of character loss observed in decay experiments. In polychaetes, for example, the cuticle and chaetae persist in decay experiments for many weeks [52], while muscle tissue and digestive organs are readily lost. In contrast, fossil polychaetes show that complete myoanatomy may survive when conditions favour extensive phosphatisation [85] while decay resistant cuticular features such as chaetae may be absent or poorly preserved [84]. In extreme cases, characters that decay rapidly are preserved to the exclusion of characters that undergo little degradation on a laboratory timescale [84].

Pyritisation, like phosphatisation, although relatively rare, can preserve the original three-dimensional morphology of structures that normally decay. Examples include the appendages and eggs of trilobites and ostracods in Beecher's Trilobite Bed in the Ordovician of New York State (Fig. 2F) [27,95], the soft parts of a diversity of marine animals in the Devonian Hunsrück Slate of Germany [96] and of the polychaete *Arkonips* from the Devonian of Ontario (Fig 3B) [97]. Pyritization of soft tissues occurs in fine-grained siliciclastic sediments that are otherwise poor in organic matter but enriched in iron [96]. In such settings, decaying carcasses provide a locus for anaerobic sulphate reduction, resulting in the production of sulphide and formation of pyrite [96,98]. Iron-enriched pore water is a prerequisite for pyritization, and may explain why pyrite framboids commonly occur in association with soft-bodied fossils from the Cambrian Chengjiang biota but are rare in similar Burgess Shale-type assemblages elsewhere in the world [98,99].

Using decay as a guide to preservation can compromise the interpretation of fossils

An overemphasis on the sequence of decay observed in experiments in interpreting soft-bodied fossils assumes that the anatomy preserved is a

reflection of original morphology tempered by decay loss (the 'rotting away' of characters) [18-20,61]. Decay experiments on a diversity of taxa (Supplementary Table 1) have shown that 'stemward slippage' [22] appears to be a peculiarity of chordates. This is perhaps not surprising as there is no *a priori* reason why derived characters should be more or less decay prone than others – in arthropods, for example, morphological characters sheathed in cuticle have a high preservation potential, and cuticular characters are subject to evolutionary change at all levels in the systematic hierarchy of Arthropoda.

The too literal interpretation of fossils as representing a stage of decay in the laboratory risks ignoring other factors that affect the loss or preservation of morphological features. Although we need to be careful not to overinterpret the anatomy of soft-bodied fossils, we cannot assume that because features decay rapidly in experiments, they can never be fossilised, particularly if the fossil evidence itself is compelling. Animals that lack an extracellular cuticle, such as the soft bodied mollusc *Odontogriphus* [100], the enteropneusts [63] and the chordate *Pikaia* [59] are preserved in the Burgess Shale, and chaetognaths are preserved in both the Burgess Shale [101] and Chengjiang biotas [102]. Although the body outlines of fossil chaetognaths are poorly defined [102], those of *Odontogriphus*, *Spartobranchus*, *Oesia* and *Pikaia* are clearly preserved, indicating that structures that lack the extracellular materials in cuticles nonetheless survive in Burgess Shale-type deposits [*contra* [103]]. Other decay-prone characters, such as features of the digestive system, are preserved as reflective films (representing carbon) in both Sirius Passet and Burgess Shale fossils . The identification of features of the digestive system is relatively straightforward based on their position and morphology (e.g., often highly detailed anatomy preserved in midgut glands) and has caused little controversy, even though decay studies suggest that they should have a very low preservation potential [20]. Early authigenic mineralization often confers a greater degree of three-dimensionality to fossilised guts than to more decay-resistant features, including cuticle.

Yang *et al.* [104] identified well organised segmental ganglia in a total group euarthropod from the Chengjiang biota. Sansom [20] argued that this

interpretation was implausible based on the rapid loss of nervous system morphology in his decay experiments on priapulids. However it is difficult to conceive how shrinkage of other anatomical features could generate the well organized features [105-107] and serially repeated structures [104] interpreted as fossil nervous systems. Shrinking a cuticle would not be expected to generate a rope-ladder morphology that was the primary basis for identification as a nerve cord.

Decay experiments on priapulid worms have shown that carcasses develop pronounced asymmetrical bulges as they decay in seawater, presumably as a result of fluid and gas build up (e.g. [20], figures 3,4). It does not necessarily follow, however, that the relative body dimensions of fossil priapulids are likewise distorted and should be excluded from phylogenetic analysis. Priapulid specimens from the Burgess Shale are approximately symmetrical, presumably due to the effect of confining sediment, even where separation of the body wall from the cuticle indicates that some decay has taken place [46]. The familiar dark stains at the anterior and posterior of Burgess Shale fossils are not due to compaction, but reflect the escape of decay fluids; distortion of the body shape was limited by the confining effect of the sediment. Similar considerations apply to the decay of onychophorans. Asymmetrical bulges and distortion of the body observed in experiments [19] have not been observed in fossil lobopodians, even where the internal anatomical features have separated from the cuticle indicating that decay has taken place, such as in *Antennacanthopodia* [108]. Lobopodian fossils typically show no evidence of distortion, suggesting that build-up of decay fluids (sometimes evidenced by dark stains) is sometimes accommodated by leakage rather than deformation of the body.

The claws and jaws of onychophorans are decay resistant and, on that basis, their absence in *Helenodora* from the Carboniferous Mazon Creek deposit has been argued to be primary [18]. Likewise *Helenodora* is thought to have lacked slime papillae; they too are absent, and their preservation potential should be similar to other cuticular structures such as dermal papillae and limbs. The presence or absence of slime papillae is significant, as their presence in *Helenodora* would indicate a phylogenetic position close to the crown group of

Onychophora. A recently described onychophoran from Montceau-les-Mines, France, a similar late Carboniferous assemblage preserved in concretions, preserves slime papillae and crown group-like antennal annuli, papillae and trunk plicae but not claws [109]. Onychophoran claws have a deep evolutionary origin evidenced by their presence in stem onychophorans (lobopodians) such as *Hallucigenia* from the Cambrian Burgess Shale [110]. The presence of an otherwise crown onychophoran-like suite of characters without claws suggests that other mechanisms may explain their absence in both Carboniferous taxa, such as rapid shedding from the body soon after death, as observed in fossils in amber [111]. Furthermore, the highly retractile nature of slime papillae renders them difficult to observe, even with near pristine preservation of external cuticular anatomy and the use of synchrotron tomography [111], so they too may also have been present in *Helenodora*, but are not preserved.

Experiments on cyclostomes and invertebrate chordates [22,64] showed that the notochord persists until the latest stages of decay (Fig 4). Nonetheless the notochord is apparently absent in several taxa from Mazon Creek [67] even though other characters indicate that they belong to the vertebrate crown group, and therefore possessed a notochord. The notochord is also absent in *Haikouichthys*, a total group vertebrate from the early Cambrian (Fig 4.), despite the preservation of characters such as eyes, gill pouches, and a dorsal fin, which disappear more rapidly in decay experiments, but clearly indicate a phylogenetic position consistent with the presence of a notochord [22,64,112]. *Haikouichthys* preserves a chimaeric assemblage of decay prone and decay resistant characters rather than corresponding to a particular decay stage (Fig. 4). Likewise, the notochord is poorly preserved or equivocal in *Pikaia* and *Haikouichthys*, whereas other decay prone characters including the eyes and nasal capsules are preserved in both taxa as well as the liver and heart in *Metaspriggina*, a vertebrate from the Burgess Shale [113]. Thus explaining the characters preserved in these fossils requires an appeal to more than just simply decay resistance. Furthermore, the quality of preservation varies among individuals of the same taxon, between taxa preserved in the same bed and between fossil assemblages, demonstrating that variations in environmental parameters

determine the quality of preservation at different temporal and spatial scales [34,84].

Conclusions

The route of a carcass from death to discovery as a fossil is complex, involving the interplay of rapid burial, decay, precipitation of tissue-replicating minerals such as apatite and pyrite, and subsequent changes such as diagenesis that occur on a geological time scale. All of these processes contribute either to the preservation or loss of biological information encapsulated in these fossils. Although decay experiments in artificial seawater provide an important null model for understanding the processes that impact soft-tissue preservation [21,24], fossils do not represent simple stages in the decay process. Decay-prone tissues (e.g. muscle tissue) can be preserved by authigenic mineralisation even when more decay resistant tissues are lost. Conversely more decay-resistant structures (such as the notochord and certain polychaete jaws) often do not survive longer-term alteration. The assumption that decay resistant structures fossilise while decay prone structures do not [19,20] does not apply to every soft-bodied fossil: factors other than decay also control preservation and exceptional circumstances can result in counterintuitive results (such as muscle being more pristine than cuticle). Understanding and interpreting fossils requires consideration of geological as well as biological processes, and the evidence provided by the fossils themselves and their preservational context is critical.

Figure 1. The long journey from live organism to the eventual rendition into, and discovery, as a fossil.

Figure 2. Exceptionally preserved fossils. A: *Sinosauropteryx prima*, a feathered dinosaur from the Cretaceous Jehol Biota, preserving melanised tissues (feathers, eyes and abdominal organs). B: *Aquilonifer spinosus,* a Silurian arthropod preserved in three dimensions in volcanic ash-hosted carbonate concretions from Herefordshire. Image at left shows a surface captured during serial grinding, image at right shows a three dimensional reconstruction from serial photographs [114]. C: *Belemnotheutis antiquus,* a Jurassic stem group decabrachian (belemnoid) from Christian Malford, Wiltshire, U.K., preserving creamy coloured musculature replaced by calcium phosphate and organic arm hooks. D: Fossil *Anolis* lizard preserved in Miocene Dominican amber [115]. Image at right is a photograph of specimen, image at left shows 3D reconstruction using micro CT. E: *Haootia quadriformis,* a possible medusozoan from the Ediacaran of Newfoundland. F: pyritised specimens of the trilobite *Triarthrus eatoni* with preserved limbs from the Late Ordovician Beecher's Trilobite Bed, New York, State. Image credits to the authors, except C (Jonathan Jackson, NHM) D (Russell Garwood and Emma Sherratt) E (Alex Liu), F (David Rudkin).

Figure 3. Same organism, different pathways of preservation. A-D show epibenthic polychaete worms preserved through different key preservational pathways. A: preservation as a carbonaceous compression, *Canadia spinosa*, Middle Cambrian Burgess Shale of British Columbia. B: three dimensional preservation in pyrite, *Arkonips topororum,* Devonian of Ontario. C: three dimensional preservation of mainly muscle tissue in calcium phosphate, *Rollinschaeta myoplena,* Late Cretaceous, Lebanon. Inset image shows SEM photomicrograph of preserved muscle fibres. D: entombment in an ironstone concretion, *Fossundecima konecniorum,* Mazon Creek, Late Carboniferous, Illinois. E: tissue specificity of taphonomic pathways in *Marrella splendens* from

the Burgess Shale. Image at left shows photograph of specimen ROMXXXX. Images at right show SED-EDX elemental maps of region encompassed by the white box in the photograph where the intensity of the colour indicates elemental abundance. Structures preserved as carbon films are highlighted in the C map, structures preserved by clay minerals are highlighted in the Al, Si and K maps, pyritised structures are highlighted in the Fe and S maps and structures preserved as apatite (calcium phosphate) are highlighted in the Ca and P maps.

Figure 4. Characters resistant to experimental decay do not closely match characters preserved in fossils. Instead, fossils preserve a combination of decay resistant and decay prone characters. A: Schematic anatomy of extant lamprey (*Lampetra*) (top) and lancelet (*Branchiostoma*) (bottom). B: Reconstruction of lamprey in an advanced state of decay (decay stage 5, sensu Sansom et al. [22]). C: Drawing (top; after Zhang and Hou [116]) and photograph (bottom) of an exceptionally preserved fossil chordate, *Haikouichthys*. Photograph by Peiyun Cong, Yunnan University and NHM, London.

BOX 1

The late Ediacaran (~580-541Ma) is a unique period in earth history, predating the major radiation of the animal phyla in the Cambrian, when assemblages of macroscopic, soft-bodied organisms were preserved as high relief casts and molds, sometimes with hundreds of individuals on a bedding plane [31,117,118]. Although most common in the Ediacaran, this taphonomic window persists until the Devonian [31]. Such fossils occur in a range of depositional environments, including deep marine basins, marginal marine settings, storm influenced shore faces and shelf carbonates [118]. Specimens may retain sub-millimetric details of mostly external, but sometimes internal [119], anatomy, and are sometimes three dimensionally preserved within beds [120]. These Ediacaran organisms were buried rapidly in event beds, either by storm deposits, turbidites,

volcaniclastic events or ash falls, depending on locality [118]. Ediacaran deposits were interpreted as census 'snapshots' [121], but it is now recognized that they can include partially decayed individuals that died prior to the event that smothered the sea floor [25]. The preservation of abundant *in situ* carcasses reflects limited or absent macrophagous scavenging during the Ediacaran [25]. Although the mechanism that led to the preservation of these organisms remains controversial, and a single explanation may not apply to all localities, most models involve sealing the sediment. Candidates include rapidly forming pyrite crusts referred to as 'death masks' [30,118], microbial mats[30], clay mineral templating [122] and early silicate cementation [31].

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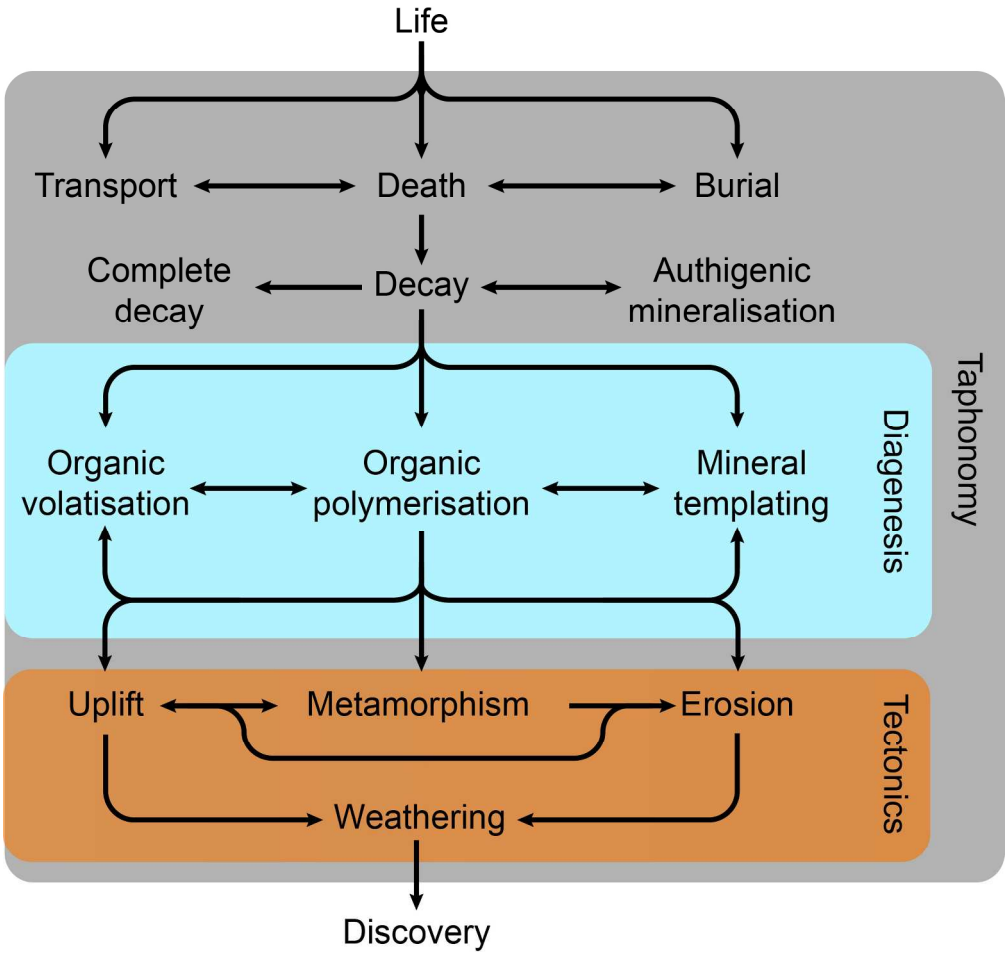

Figure 1. The long journey from live organism to the eventual rendition into, and discovery, as a fossil.

209x198mm (300 x 300 DPI)

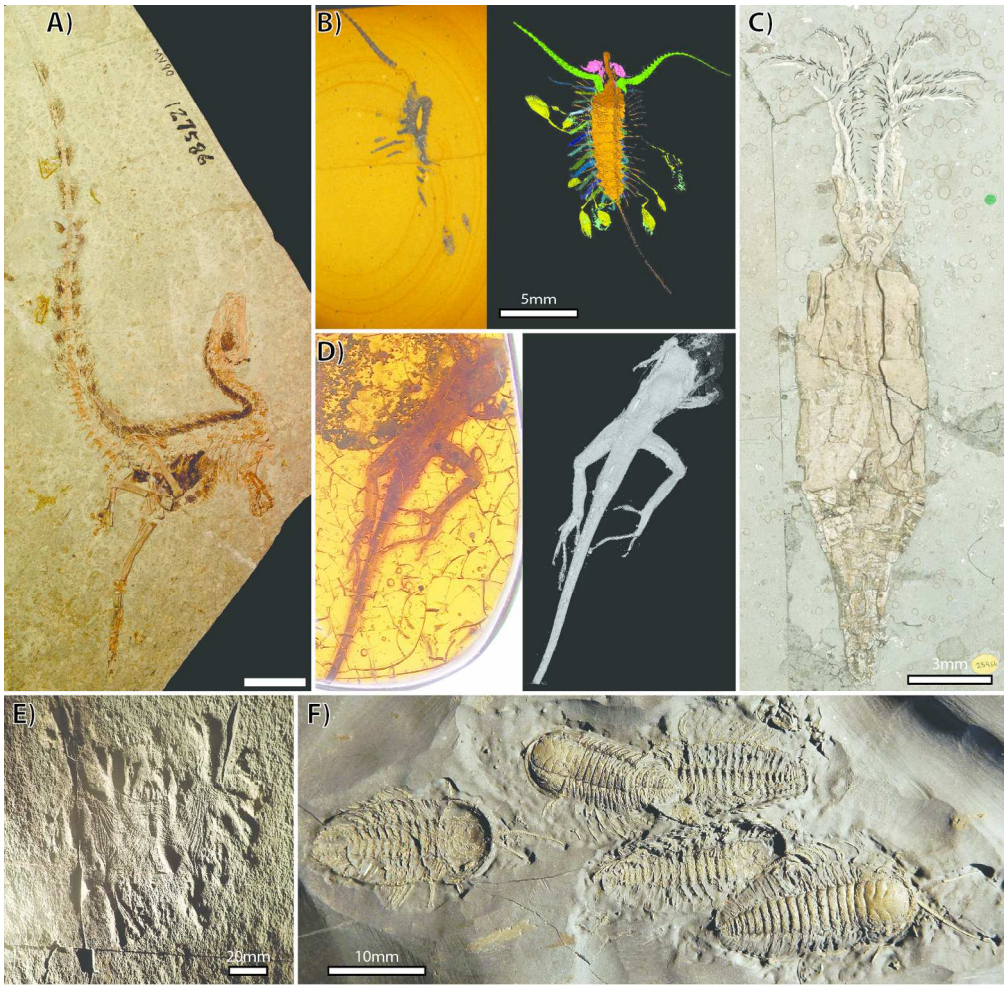

Figure 2. Exceptionally preserved fossils. A: Sinosauropteryx prima, a feathered dinosaur from the Cretaceous Jehol Biota, preserving melanised tissues (feathers, eyes and abdominal organs). B: Aquilonifer spinosus, a Silurian arthropod preserved in three dimensions in volcanic ash-hosted carbonate concretions from Herefordshire. Image at left shows a surface captured during serial grinding, image at right shows a three dimensional reconstruction from serial photographs [114]. C: Belemnotheutis antiquus, a Jurassic stem group decabrachian (belemnoid) from Christian Malford, Wiltshire, U.K., preserving creamy coloured musculature replaced by calcium phosphate and organic arm hooks. D: Fossil Anolis lizard preserved in Miocene Dominican amber [115]. Image at right is a photograph of specimen, image at left shows 3D reconstruction using micro CT. E: Haootia quadriformis, a possible medusozoan from the Ediacaran of Newfoundland. F: pyritised specimens of the trilobite Triarthrus eatoni with preserved limbs from the Late Ordovician Beecher's Trilobite Bed, New York, State. Image credits to the authors, except C (Jonathan Jackson, NHM) D (Russell Garwood and Emma Sherratt) E (Alex Liu), F (David Rudkin).

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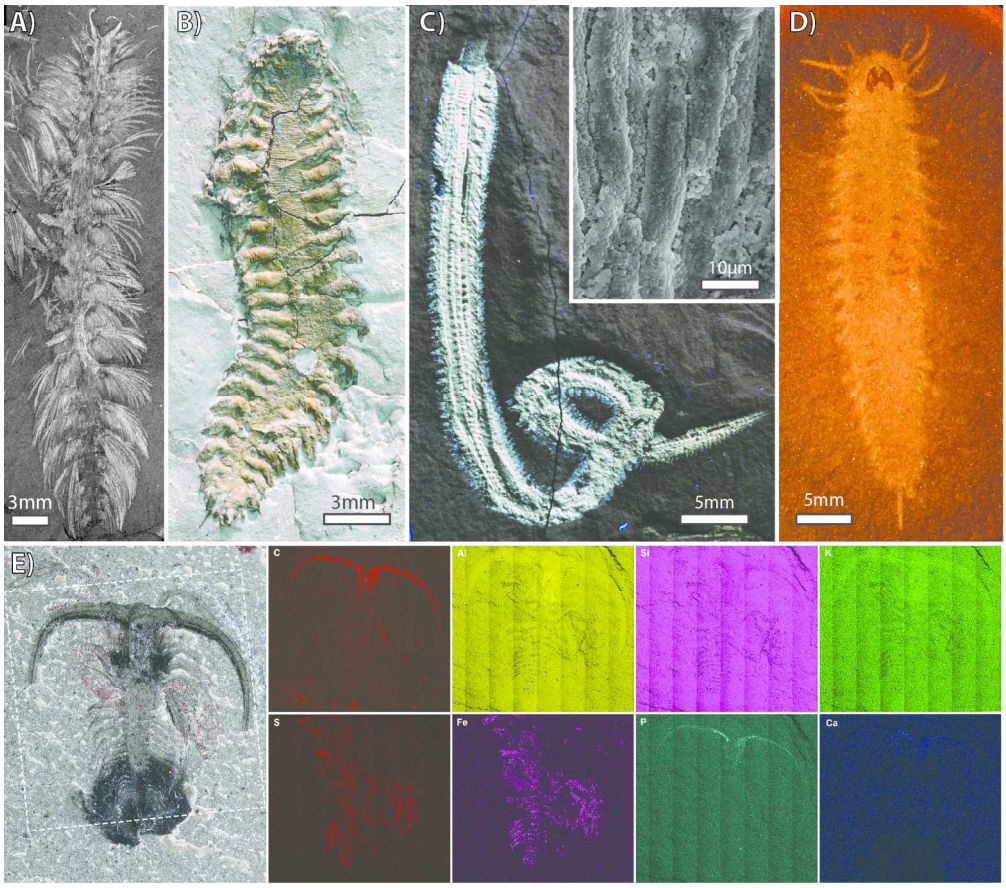

Figure 3. Same organism, different pathways of preservation. A-D show epibenthic polychaete worms preserved through different key preservational pathways. A: preservation as a carbonaceous compression, Canadia spinosa, Middle Cambrian Burgess Shale of British Columbia. B: three dimensional preservation in pyrite, Arkonips topororum, Devonian of Ontario. C: three dimensional preservation of mainly muscle tissue in calcium phosphate, Rollinschaeta myoplena, Late Cretaceous, Lebanon. Inset image shows SEM photomicrograph of preserved muscle fibres. D: entombment in an ironstone concretion, Fossundecima konecniorum, Mazon Creek, Late Carboniferous, Illinois. E: tissue specificity of taphonomic pathways in Marrella splendens from the Burgess Shale. Image at left shows photograph of specimen ROMXXXX. Images at right show SED-EDX elemental maps of region encompassed by the white box in the photograph where the intensity of the colour indicates elemental abundance. Structures preserved as carbon films are highlighted in the C map, structures preserved by clay minerals are highlighted in the Al, Si and K maps, pyritised structures are highlighted in the Fe and S maps and structures preserved as apatite (calcium phosphate) are highlighted in the Ca and P maps.

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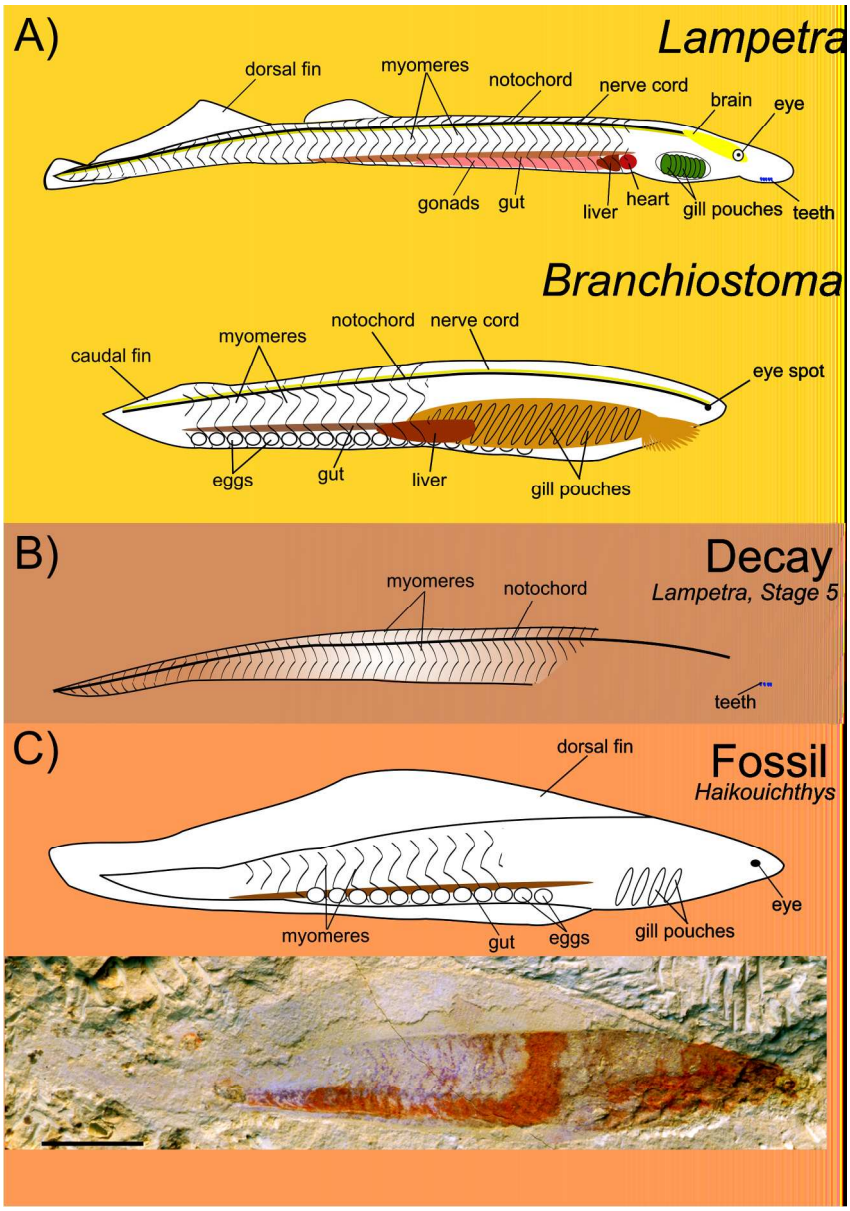

Figure 4. Characters resistant to experimental decay do not closely match characters preserved in fossils. Instead, fossils preserve a combination of decay resistant and decay prone characters. A: Schematic anatomy of extant lamprey (Lampetra) (top) and lancelet (Branchiostoma) (bottom). B: Reconstruction of lamprey in an advanced state of decay (decay stage 5, sensu Sansom et al. [22]). C: Drawing (top; after Zhang and Hou [116]) and photograph (bottom) of an exceptionally preserved fossil chordate, Haikouichthys. Photograph by Peiyun Cong, Yunnan University and NHM, London.